



Group and Mass Recruitment in Ant Colonies: the Influence of Contact Rates

ERIC BONABEAU*§, GUY THERAULAZ† AND JEAN-LOUIS DENEUBOURG‡

**Santa Fe Institute, 1399 Hyde Park Road, Santa Fe, NM 87501, U.S.A.,*

†*Laboratoire d'Ethologie et de Psychologie Animale, CNRS-UMR 5550, Université
Paul Sabatier, 118 route de Narbonne, 31062 Toulouse Cédex, France*

‡*Unit of Theoretical Behavioural Ecology, Service de Chimie-Physique, CP 231,
Université Libre de Bruxelles, Boulevard du triomphe, 1050 Brussels, Belgium*

(Received on 25 April 1997, Accepted in revised form on 2 July 1998)

The influence of contact rates on the efficiency (the ability to exploit a profitable environment) and flexibility (the ability to track a changing environment) of foraging in ants is studied theoretically in the case where foraging relies on a mixture of group and mass recruitment. It is shown that a combination of efficiency and flexibility can be reached across a range of group sizes if (1) mass recruitment is combined with a low level of group recruitment, and (2) contact rates are weakly regulated. These results are discussed in relation to empirical work.

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1. Introduction

1.1. GROUP SIZE, INFORMATION TRANSFER AND CONTACT RATES

How does information spread among members of a social group of animals, and how is it collectively processed? Being able to answer these two important questions could prove extremely insightful to understand the evolution and maintenance of social life, as collective information processing and transfer may be the essential factors that contributed to the success of animal societies, particularly social insects. In a recent study, Pacala *et al.* (1996) have examined the effects of group size on information transfer and task allocation in social groups. In their model, individuals make

decisions about which task to perform depending both on environmental stimuli and interactions among themselves. Although in principle larger groups may be more efficient than smaller ones at tracking a changing environment when rates of interactions per individual increase with group size, there may be an overload of social information in very large groups, so that individuals keep performing tasks which are less profitable. Pacala *et al.* (1996) predicted that in order to balance optimally the flow of information from environmental stimuli and social exchanges (for example, in social insects, antennation, mandibular contacts, trophallaxis, etc.) across a range of group sizes, ants should regulate their *per capita* rates of social interaction.

Surprisingly, however, Pacala *et al.* (1996) did not test the effects of regulating contact rates in

§Author to whom correspondence should be addressed.

their own model. Nor did they examine the case where returns associated with performing a given task increase with the number of individuals that perform this task: in such a situation, for two equally profitable tasks, individuals should all perform one of these tasks and not the other. The aim of this paper is to illustrate, within the context of recruitment-based foraging in ant colonies, how the regulation of contact rates affects the ability of a group to (1) allocate most of its members to one task (exploitation), and (2) at the same time, track a changing environment (flexibility). We will show that, despite possible conflicting constraints between exploitation and flexibility, some foraging strategies that combine a small amount of group recruitment with mass recruitment can be optimal from both viewpoints; this optimality is achieved only if the colony is able to regulate contact rates at a specific level.

1.2. RECRUITMENT STRATEGIES USED BY ANTS IN RELATION WITH FORAGING ACTIVITIES

Many species of ants have trail-laying/trail-following behavior when foraging: individuals deposit pheromone as they return from the food source (sometimes also as they go to the source, or even as they explore the environment), and foragers follow such pheromone trails. The process whereby an ant is influenced towards a food source by another ant or by a chemical trail is called recruitment. In short, there are three basic types of recruitments in ants (see Beckers *et al.*, 1989 for species-specific references): tandem recruitment (TR: e.g. *Leptothorax [unifasciatus, acervorum, etc.]*, *Camponotus sericeus*, *Pachycondyla caffraria*), whereby an individual signals to another one by direct physical interaction that it found a food source; group recruitment (GR: e.g. *Camponotus socius*, *Tetramorium impurum*, *Tetramorium caespitum*, *Tetramorium bicarinatum*), in which chemical signalling by one recruiting individual has the effect of effectively recruiting a few individuals; and mass recruitment (MR: e.g. *Lasius niger*, *Linepithema humile*, *Tetramorium erraticum*), which is performed through independent trail-laying and trail-following behaviors. While the first two strategies involve a leader that guides another individual or a group of

individuals to the food source, mass recruitment is “anonymous”.

Group recruitment is usually associated with mass recruitment (Beckers *et al.*, 1989; de Biseau *et al.*, 1994). The first foragers that have found a food source lay trail as they come back to the nest, invite nestmates to the food source, these nestmates lay trail as they come back to the nest, so that a significant pheromone trail starts to appear after some time. Mass recruitment owing to the trail takes over.

These different types of strategies lead to different responses in the following situations (Beckers *et al.*, 1990; de Biseau *et al.*, 1991):

(1) when the colony is offered two food sources of similar quality simultaneously at equal distance from the nest, it can either exploit both sources symmetrically (TR) or break the symmetry between the sources and exploit one source preferentially (GR + MR, MR);

(2) when one source is richer, some colonies still exploit both sources virtually symmetrically (TR), while others exploit the best source (GR + MR, MR) thanks to the ability of individuals to modulate the amount of trail laying (this phenomenon has been observed in several species, see Hantgartner, 1969, 1970; Cammaerts, 1977; Crawford & Rissing, 1983; Breed *et al.*, 1987; Verhaeghe, 1982);

(3) finally, when the richer source is presented to the colony a certain amount of time after the poorer source, some colonies once again exploit both sources symmetrically (TR), others are able to shift most of their foraging activity to the richer source (GR + MR), and others are trapped on the trail to the poor source and are unable to switch to the richer source (MR).

What is the colony-optimal pattern of worker allocation to the food sources? In the case of two food sources of different quality, all foragers should be allocated to the richer source. If there are increasing returns in the sense that, for equally profitable sources (in terms of source quality, quantity, distance from the nest, etc.), it is better to concentrate the colony's activity on one source (it may be the case because there is predation or competition: for example, such a strategy may offer a better protection of the path to the food source), then the colony-optimal

allocation of foragers would be approximated by:

(A) all or most foragers exploit one source (arbitrarily chosen) when both sources are similar; and

(B) all or most foragers exploit the richer source when a source is richer.

In these hypothetical ecological conditions, optimality would be reached with a combination of efficiency (the ability to focus on one source) and flexibility [the ability to shift the foraging activity and allocate most foragers to the richer source—if the quality difference justifies such a shift (Bonabeau, 1996)]. In the next section, we shall study if, and under what conditions, these two optimal strategies (A) and (B) can be implemented with a single set of behavioral parameters. One important question is whether and to what extent contact rates should be regulated.

Note that other types of foraging strategies, such as individual foraging, group raiding, the use of trunk trails, or group hunting will not be considered here (Beckers *et al.*, 1989). Some of these strategies rely on recruitment in one form or another. Besides the fact that recruitment processes are extremely widespread in social insects, they are particularly interesting in the context of collective information processing in animal colonies because they explicitly involve direct or indirect exchanges of information among individuals. The model that will be described and analysed in the rest of this paper is based on previous models of recruitment in ants (Deneubourg *et al.*, 1983, 1987; Verhaeghe & Deneubourg, 1983; Pasteels *et al.*, 1987; Deckers *et al.*, 1990), but explicitly takes into account the possibility of contact rate regulation, thereby adding a whole new dimension to these models. Including the effect of contact rate regulation, following Gordon's original idea (Gordon *et al.*, 1993; Gordon, 1996; Pacala *et al.*, 1996), is important because contact rates influence what social information is available to individuals to make decisions, here foraging decisions. The collective behavior of the colony, and its reproductive efficiency, results from many such individual decisions.

2. Models for Mass and Group Recruitment when Two Food Sources are Offered to the Colony

2.1. RECRUITMENT RATE

Let N be the total number of potential foragers in the colony (that is, the number of individual ants which may be involved in exploiting a food source; some individuals may never, or very rarely, do so because they are engaged in other tasks), and X the number of individuals exploiting a given food source. Let λ be the effective recruitment rate of new foragers to that food source. λ can be assumed to be the product of two factors: (1) the probability \mathbf{a} that an individual who is not exploiting the food source will be stimulated to do so when it meets an individual exploiting the food source, and (2) the probability of encounter per unit time, which we assume to be proportional to N^{-z} (the multiplicative constant, which includes the effects of the size of the foraging area, food source quality, the speed of motion of individuals, their physiological states, can be integrated into \mathbf{a}). $\mathbf{a}N^{-z}$ is therefore the number of successful recruitments per forager per unit time. The second factor depends on the regulation of contact rates: if $z = 0$, the number of interactions per unit time between a given forager and potential recruits increases as N , whereas if $z = 1$, this number remains constant.

Let us examine why and how the effective recruitment rate λ should depend on N . Let S be the area explored per non-foraging individual per unit time, Ω the total recruitment area, and $\rho = N/\Omega$ the global spatial density of ants. Let us first assume that Ω does not depend on N : this constraint can be forced in experiments but may not be true in the field. Within one time unit, assuming no regulation of contact rates, a randomly walking individual meets on average $S\rho = SN/\Omega$ other individuals, but only SX/Ω foragers. If SX/Ω is not significantly greater than 1, the probability of a non-foraging individual being recruited is given by $\alpha SX/\Omega$ where α is the ability of an ant that exploits the food source to stimulate any remaining potential forager to follow her to that food source. α can reasonably be assumed to be independent of N : it is a property of individuals, and may depend mainly on physiological factors (influenced by tempera-

ture, light, or the level of satiation of the colony). In conclusion, if Ω does not depend on N , and if there is no other mechanism leading to some kind of regulation of contact rates, $\lambda = \alpha S/\Omega$ is independent of N . Let us now assume that contact rates per individual increase sublinearly, instead of linearly, as a function of group size N , because some of the factors (S , Ω , or even α) that were assumed to be independent of N do in fact depend on N . Pacala *et al.* (1996) suggested a continuum of possible levels of regulation described by a single parameter z : N^{1-z} is the *per capita* rate of social interaction as a function of group size (neglecting a multiplicative constant). $z = 0$ corresponds to the case of no regulation at all (Deneubourg *et al.*, 1983, 1987; Verhaeghe & Deneubourg, 1983; Pasteels *et al.*, 1987). At the other extreme, $z = 1$ corresponds to a perfect regulation of contact rates. This explains why the effective recruitment rate λ can be written $\lambda = aN^{-z}$ where a is a factor of recruitment efficiency that does not depend on N .

2.2. MODEL

Let us now assume that individuals lay pheromone trails, and that two food sources are presented to the colony. In a number of species, the accuracy with which recruitment is performed depends not only on the recruitment rate but also on the ability of a given ant to follow a trail, which in turn depends on the strength of the trail. Let Y be the average pheromone concentration on the trail. Deneubourg *et al.* (1987) and Pasteels *et al.*, (1987) suggest that the degree of precision of trail following is given by $F = (g + Y^2)/(h + Y^2)$ (where $g < h$ are two parameters which characterize the efficiency of the trail at the beginning of recruitment) in the case of mass recruitment. In the case of group recruitment, $F = k$ is a constant related to the quality of the food source. A given combination of group and mass recruitment can be characterized by a coefficient $\beta \in [0,1]$ such that $F = (1 - \beta)k + \beta(g + Y^2)/(h + Y^2)$. We must also take into account ‘‘exploring’’ or ‘‘lost’’ ants. We assume that the two competing food sources are at the same distance from the nest. At fixed N , the equations for all

variables, neglecting fluctuations, are then given by

$$\frac{dX_i}{dt} = a_i(X_i/N^z) \left(N - E - \sum_{i=1}^n X_i \right) F_i + cE - bX_i, \quad (1)$$

$$\frac{dE}{dt} = \left(\sum_{i=1}^n a_i(1 - E_i) (X_i/N^z) \right) \times \left(N - E - \sum_{i=1}^n X_i \right) - ncE - pE, \quad (2)$$

$$\frac{dY_i}{dt} = \eta_i X_i - \chi Y_i, \quad (3)$$

$$F_i = (1 - \beta)k_i + \beta \frac{g + Y_i^2}{h + Y_i^2}, \quad (4)$$

where n is the number of sources, E the number of exploring ants, X_i the number of ants exploiting source i ($i = 1, 2$ in the present case), and $N - E - X_i$ the number of foragers in the nest, Y_i the amount of pheromone deposited on the trail to source i , η_i the rate of pheromone deposition of an individual exploiting source i , F_i the fraction of source i recruits that effectively reach source i , $1 - F_i$ the fraction of source i recruits that lose the trail, a_i the recruitment rate of source i , $1/p$ the time taken by explorers before returning to the nest if they do not find any source, c the probability that any source is found by chance by an explorer, $1/b$ the average time spent by a foraging at the source (before becoming inactive or switching tasks), $1/\chi$ is the average lifetime of the pheromone. Higher values of a_i and k_i correspond to higher-quality sources. It is assumed that g , h , and η_i do not depend on the food source.

Equations (1), (2) and (3) give an average description of the process and, although the formulation is continuous, the equations may be better understood in discrete time. It is assumed that within Δt , the X_i individuals who actually exploit the food source i recruit $a_i(X_i/N^z)(N - E - \sum_{i=1}^n X_i) \Delta t$ individuals, but only a fraction F_i , which depends on the amount of pheromone deposited, reaches the source. Everything happens within Δt , so that at $t + \Delta t$, the

effective number of individuals exploiting source i is given by $X_i(t) + (a_i(X_i/N^2)(N - E - \sum_{i=1}^N X_i) F_i) \Delta t$. It is assumed that the fraction $1 - F_i$ of ants that were recruited between t and $t + \Delta t$ lost the trail within the same time interval. Not making this assumption would introduce unnecessary complications, as one would have to model how much time it takes before a recruited ant gets lost. If Δt is sufficiently large, the assumption is valid. The continuous formulation is more elegant, but the discrete formulation yields identical results.

3. Results

We consider only two cases:

(1) *two food sources of identical quality are presented simultaneously to the colony.* X_w will denote the number of foragers exploiting the winning source, that is, the most exploited source. If both sources happen to be equally exploited, X_w is the number of foragers exploiting either one;

(2) *the better quality food source is presented to the colony after the first one has been selected.* X_1 will denote the number of foragers exploiting the first (poorer) source, and X_2 the second (richer) source.

Let us first study a case where N is fixed, for example $N = 295$ (but the results obtained for this value are fairly general, except for mass recruitment). The parameters [suggested by Verhaeghe & Deneubourg (1983) to account for experimental observations in *Tetramorium impurum*] used in the numerical integration of eqns (1)–(4) are: $a_1 = 0.028 \text{ min}^{-1} \text{ indiv}^{-1}$, $a_2 = 0.03 \text{ min}^{-1} \text{ indiv}^{-1}$, $b = 0.017 \text{ min}^{-1}$, $c = 0.018 \text{ min}^{-1}$, $k_1 = 0.58$, $k_2 = 0.6$ (F , being a fraction, is dimensionless), $\chi = 1 \text{ min}^{-1}$, $g = 25 \text{ q}^2$, $h = 35 \text{ q}^2$, and $\eta_1 = \eta_2 = 1 \text{ q indiv}^{-1} \text{ min}^{-1}$, where q is a typical amount of pheromone laid by an individual per unit length (for example, $q = 10^{-15} \text{ g cm}^{-1}$). The study will focus on the effects of varying β and z .

3.1. MASS RECRUITMENT

All figures represent stationary values of X_w , X_1 and X_2 , that is, values reached at equilibrium after transients have died out. Figure 1 shows the

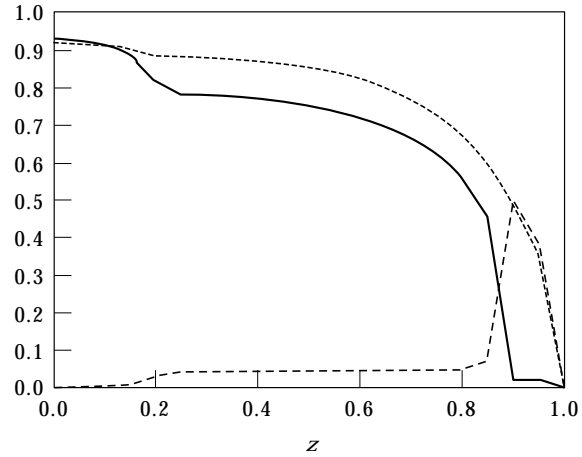


FIG. 1. X_1/N (—), X_2/N (---) and X_w/N (.....), as a function of N and z for $\beta = 1$ (MR), $N = 295$, $a_1 = 0.028 \text{ min}^{-1} \text{ indiv}^{-1}$, $a_2 = 0.03 \text{ min}^{-1} \text{ indiv}^{-1}$, $b = 0.017 \text{ min}^{-1}$, $c = 0.018 \text{ min}^{-1}$, $k_1 = 0.58$, $k_2 = 0.6$, $\chi = 1 \text{ min}^{-1}$, $g = 25 \text{ q}^2$, $h = 35 \text{ q}^2$, and $\eta_1 = \eta_2 = 1 \text{ q indiv}^{-1} \text{ min}^{-1}$.

case of complete mass recruitment (MR) ($\beta = 1$) for z varying between 0 and 1. It can be seen that X_w is maximal [optimal: condition (A)] when $z = 0$ (no control of contact rates). On the other hand, the value of z that is closest to optimality [condition (B): X_2 large and X_1 small] in the case of a richer source presented after the low-quality source is $z = 0.9$ (almost perfect regulation of contact rates). When pheromone is used as a medium of social communication, contact rates seem difficult to regulate, or more precisely, the level of social communication seems difficult to regulate in the context of foraging. Therefore, colonies resorting to MR are certainly better characterized by z close to 0. It follows that such colonies should be able to concentrate most of their foraging activity on a food source, but should also be unable to shift their activity to a better source when it is presented. This result is perfectly consistent with the observation of mass recruiting species.

3.2. MASS AND GROUP RECRUITMENT

Figure 2 is similar to Fig. 1, but for a small level of group recruitment (GR) ($\beta = 0.8$). It can be seen that there exists a value of z (close to $z = 0.2$) such that both optimality conditions (A) and (B) are almost satisfied. This is due to the fact that a combination of GR and MR corresponds to a combination of efficiency and

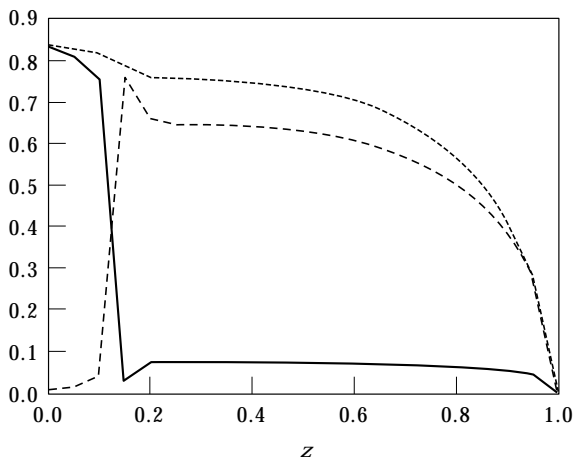


FIG. 2. Same as Fig. 1 for $\beta = 0.8$ (0.8 MR + 0.2 GR).

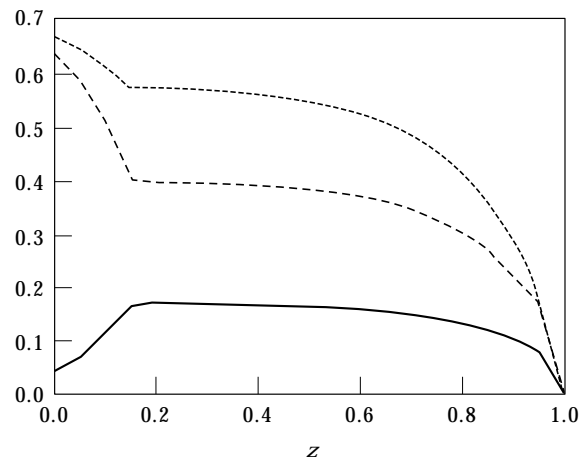


FIG. 4. Same as Fig. 1 for $\beta = 0.4$ (0.4 MR + 0.6 GR).

flexibility. It is easy to understand how MR allows for efficient foraging, by reinforcement of pheromone paths. But how does GR allow for flexibility? Lost ants can find another food source by chance, such ants can effectively recruit other ants to this new food source through GR, and then MR takes over. When the level of GR is increased (Figs 3, 4 and 5: $\beta = 0.6$, $\beta = 0.4$, $\beta = 0$), the best way of satisfying conditions (A) and (B) is with $z = 0$ (no regulation of contact rates). But there is a cost associated with GR-based strategies: inaccuracy in following the leader yields an increasing number of lost ants, and a decreasing number of individuals are actually exploiting food sources (as can be seen in Figs 3, 4, and 5: the fraction involved in exploiting the food source decreases significantly because other individuals are lost).

Therefore, although the pattern of relative allocation to the two food sources is optimal when the amount of GR exceeds some threshold and there is NO regulation of contact rates, an even better strategy consists in combining a small amount of GR (for example, $\beta = 0.8$, Fig. 2) with a small level of contact rate regulation ($z = 0.2$). It is striking that the model predicts optimality for a small level of GR, which corresponds to what is observed in real colonies that resort to GR + MR, since GR occurs only at the beginning of recruitment (de Biseau *et al.*, 1994). More specifically, it may explain the unusual combination of GR and MR observed by de Biseau *et al.* (1994) in *Tetramorium bicarinatum*, where a scout finding a food source lays a chemical trail on its way back to the nest; the efficiency of a single recruiter's trail has been

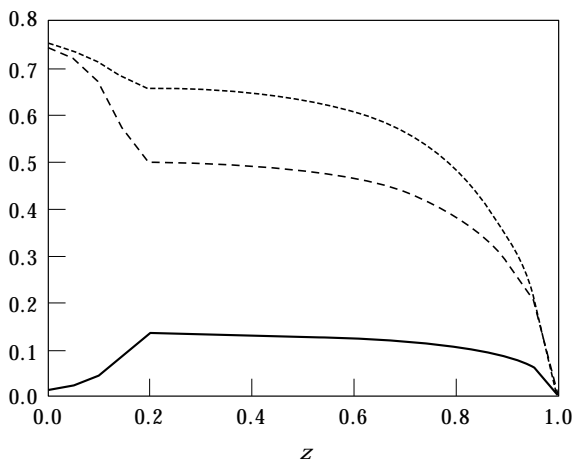


FIG. 3. Same as Fig. 1 for $\beta = 0.6$ (0.6 MR + 0.4 GR).

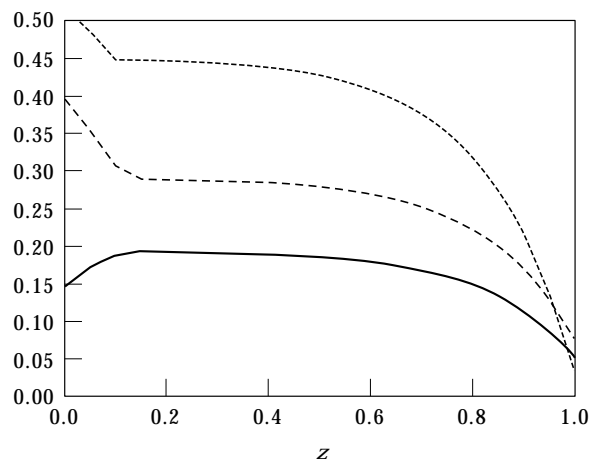


FIG. 5. Same as Fig. 1 for $\beta = 0$ (GR).

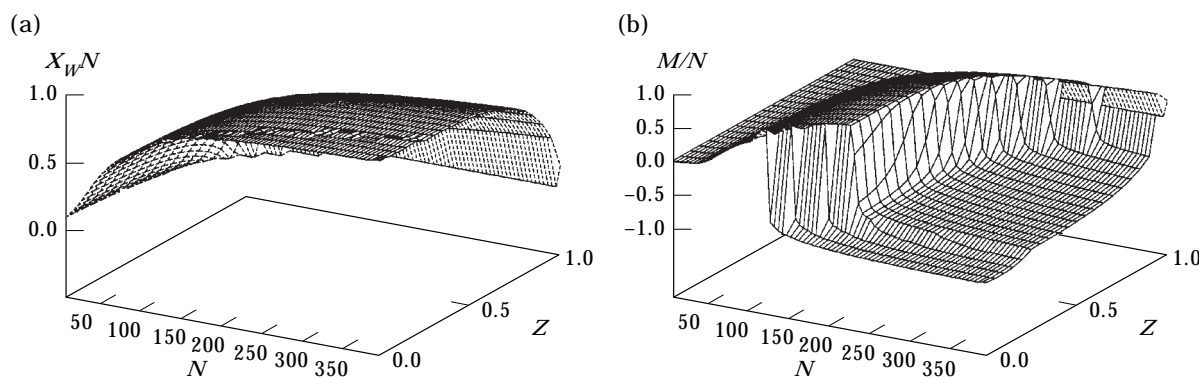


FIG. 6 (a) X_w/N as a function of N and z for $\beta = 1$ (MR). Other parameters identical to those of Fig. 1; (b) $(X_2 - X_1)/N = M/N$ for $\beta = 1$.

shown to be comparable to that of trails of purely mass-recruiting species, and larger than in other species using GR. Despite the efficiency of this trail, recruited workers prefer to follow the leader, which can be explained by the benefit of using a macroscopic amount of GR. It remains to be tested if the corresponding level of social regulation, embodied in z , is roughly of the order of $z = 0.2$. The observed *per capita* rate of social interaction (measured via the number of antennal contacts per ant) plotted against N should yield $N^{1-z} = N^{0.8}$. This prediction can be tested.

3.3. THE INFLUENCE OF N , THE NUMBER OF AVAILABLE FORAGERS

Figures 6 and 7 show how the previous results depend on N . Figure 6(a) represents X_w for $\beta = 1$ (MR) in the absence of the second source: maximal exploitation of source 1 is obtained for $z = 0$ at any N . Figure 6(b) represents $(X_2 - X_1)/N = M/N$ for $\beta = 1$ after introduction of source 2: here, the situation is slightly more complicated. The optimal allocation is obtained for a value of $z(N)$ that depends on N . For $N < 100$, the optimal $z(N)$ is close to 0, so that both conditions (A) and (B) can be satisfied simultaneously. For $100 < N < 150$, the optimal $z(N)$ increases slowly, and remains smaller than 0.3, which is still compatible with a close-to-optimal solution satisfying also approximately condition (A). However, for $N > 150$, the optimal $z(N)$ increases quickly to become of the order of 0.8 at $N = 190$. We see, here again, the conflict between conditions (A) and (B) in the

case of mass recruitment. Beckers *et al.* (1989) have suggested that species resorting to MR are characterized by colony sizes that are rarely below 1000 (reported sizes range from 10^2 to 10^5 , the average being $5 \cdot 10^3$), and the number of active foragers may be at least of the order of 200 within any foraging period. These figures indicate that for MR, values of N larger than 150 should be relevant, so that there is always a conflict between conditions (A) (which is always respected by mass-recruiting species) and (B) (which is not satisfied). Ecological constraints may explain this lack of flexibility.

If a colony resorts to mass recruitment, only in the small N region can a strategy be found that satisfies optimality conditions (A) and (B): such a strategy involves no regulation of contact rates. If N is large, as is common in *mature* colonies of mass-recruiting species, no value of z allows both foraging efficiency and flexibility. Empirical work suggests that MR does not allow flexibility, which indicates that mass-recruiting species do not regulate their contact rates. That there exists a threshold value of N below which such an absence of regulation is optimal, and above which it does not permit flexibility, is interesting from the viewpoint of colony growth: a small MR colony is both efficient and flexible, and becomes less flexible as it grows, perhaps because flexibility becomes less crucial.

Figure 7(a) represents X_w/N for $\beta = 0.8$ (GR + MR) in the absence of the second source: maximal exploitation of source 1 is obtained for $z \leq 0$ at any N . Figure 7(b) represents $(X_2 - X_1)/N = M/N$ for $\beta = 0.8$ after introduction of

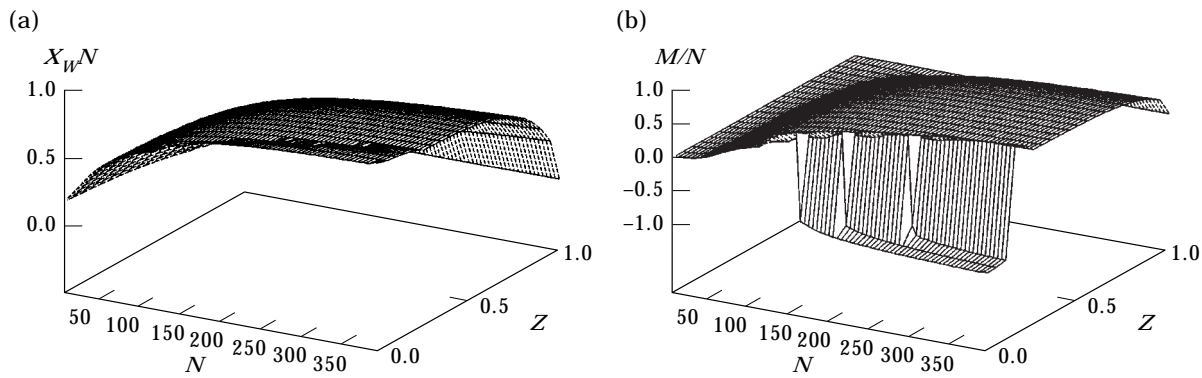


FIG. 7. (a) Same as Fig. 6(a) for $\beta = 0.8$; (b) same as Fig. 6(b) for $\beta = 0.8$.

source 2: the optimal allocation is obtained for $z = 0.2$ for any N . Reported colony sizes of species resorting to GR + MR (Beckers *et al.*, 1989) range from 2.10^2 to 10^4 , the average being of the order of 10^3 , and foraging activities may involve about 200 foragers within a foraging period, a figure that is covered by the range of values studied here. Similar results obtained for smaller values of β lead to the same conclusions as for $\beta = 0.8$: the optimal tradeoff is obtained for values of z between 0 and 0.2, but, as noticed earlier, the cost of exploration becomes higher and higher. In conclusion, a small amount of group recruitment can provide a colony with the necessary flexibility to satisfy optimality condition (B), combined with the efficiency (A) associated with MR. This optimal tradeoff can be obtained only for $z = 0.2$, and the cost of exploration is negligible if β is close to, but different from, 1. Values of χ ranging from 0.05 to 5 do not significantly alter this conclusion.

4. Discussion

4.1. LIMITATIONS OF THE MODEL

The deterministic model used in this paper is obviously an oversimplification of reality [because of parameter fluctuations, variable numbers of foragers, or other neglected factors that play a role in recruitment and foraging, such as memory, learning, etc; moreover, this model does not deal explicitly with space—for spatially explicit models, see Haefner & Crist (1994), Crist & Haefner (1994), Edelstein-Keshet *et al.*

(1995)]. It conveys, however, the essential differences that exist between mass recruitment (MR) and group recruitment (GR), and can account for behaviors observed in carefully designed experimental setups. Furthermore, when the level of contact rate regulation is varied, this model predicts colony-level behaviors that are close to those observed in real colonies.

4.2. HOW CAN CONTACT RATES BE REGULATED?

If z is different from 0, as predicted under some conditions by our model, how can contact rates be regulated in reality? Recruitment happens either in the nest, the size of which can be regulated, or in the foraging area through the trail. Nest size regulation can result from a variety of stimulating cues that trigger building behavior. For example, Franks *et al.* (1992)'s observations and models suggest that the brood might regulate building activity in *Leptothorax* by a chemical template (see also Franks & Deneubourg, 1997). How the size of the foraging area varies with colony size is an open question, although several studies suggest (although not unambiguously) that foraging area increases with colony size (Tschinkel *et al.*, 1995); competition with other colonies can limit this increase (Gordon, 1992).

Contact rate regulation based on density regulation takes place over relatively long time scales compared with the active regulation advocated by Gordon *et al.* (1993) and Gordon (1996), where workers actively avoid one another at high global density and tend to gather at low

global density. Such active regulation can take place through direct perception and can also be strongly influenced by chemical markings. The fact that the encounter rate saturates at high density may not be due to an active regulation by ants, but rather to a simple and natural side effect of the very notion of encounter: it takes some time, say t on average, to interact, so that the maximum number of encounters within an experimental period of time T is bounded by T/t , and the encounter rate cannot increase with ant density beyond that limit. Hence the observed saturation. For example, using the experimental data of Gordon *et al.* (1993), we find that the surface covered by an ant by time unit is of the order of $2 \cdot 10^{-4} \text{ m}^2 \text{ s}^{-1}$ and that the saturation of contact rates occurs at a density around 1000 ants m^{-2} , where an ant meets another ant every 5 s and therefore 36 ants within the 3 min of observation. But meeting an ant every 5 s does not leave a lot of time to interact [although Gordon *et al.* (1993) have observed that interactions last only several hundredths of a second]. Active regulation, if it occurs, has a limited range of action: even if there is active regulation, the saturation regime resulting from interaction time is reached at high density, and in fact, according to the simple calculation above, the active regulation regime may be hard to distinguish. Regulation, in this case, would result more from a natural effect due to interaction time than to an active avoidance behavior from ants. An accurate definition of the term interaction and more experimental work are needed to confirm this statement.

Contact rates may not be temporally stable, and may vary simply in response to environmental factors, such as light or temperature, or because of the level of satiation of the colony (for example, a hungry colony may explore the environment further away and at a different speed), or other endogenous factors which generate oscillations and/or synchronization (Cole, 1991; Franks *et al.*, 1990; Deneubourg & Franks, 1995). It is not absurd to think, therefore, that contact rates may vary in time and can be adjusted if necessary to make foraging more efficient or flexible depending on the physiological state and the foraging success of the colony. Finally, division of labor, the

regulation of which may rely on an appropriate level of contact rates (Gordon, 1996), is also often associated with a spatial distribution of the tasks to be performed; such a distribution exerts an influence of contact rates, that may be dependent on the task (Franks & Sendova-Franks, 1992; Sendova-Franks & Franks, 1993, 1995; Hatcher *et al.*, 1992; Tofts & Franks, 1992). Learning may also be involved in contact rate regulation, as task performance reinforces certain patterns of interaction (Theraulaz *et al.*, 1991).

4.3. CONCLUSION

In conclusion, we have studied with a model the influence of contact rates on the efficiency (the ability to exploit a profitable environment) and flexibility (the ability to track a changing environment) of foraging strategies based on group and mass recruitment in ants. This study, which is the first to deal explicitly with contact rates in the context of recruitment, suggests that a combination of efficiency and flexibility is obtained for a specific mixture of group and mass recruitment, where mass recruitment dominates over group recruitment ($\beta = 0.8$); in addition, if this combination of efficiency and flexibility is to hold across a range of forager pool sizes, contact rates, which affect the effective recruitment rate, have to be weakly regulated ($z = 0.2$). This shows that it is particularly important to take contact rates into account in models of recruitment-based foraging. In all other cases, the colony is either flexible but not able to massively exploit a food source, or vice versa. The predictions of the model are consistent with what is known about colonies that resort to mass and/or group recruitment. Finally, the model predicts that the *per capita* rate of interactions, in those species that have been empirically observed to exhibit both efficiency and flexibility, is proportional to $N^{0.8}$, a prediction that can be tested.

This work was supported in part by a grant from the GIS (Groupe d'Intérêt Scientifique) Sciences de la Cognition. E. B. is supported by the Interval Research post-doctoral fellowship at the Santa Fe Institute.

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